STUDIES ON THE TALITRIDAE (AMPHIPODA, CRUSTACEA) IN JAPAN
III. LIFE HISTORY AND BREEDING ACTIVITY OF *ORCHESTIA PLATENSIS* KRØYER[1)2)]

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With 1–8 Text-figures and 1–7 Tables

INTRODUCTION

Life histories and breeding activities of the gammaridean Amphipoda have been elucidated in many species from various view points. Many studies are directed to contribute to the biology of a species (Watkin, 1941; Amanieu, 1969; Steele and Steele, 1969–1975c; Dexter, 1971; etc.) and some have been done to afford the basis for production study of a species (Cooper, 1965; Klein, 1975) and still some are with the intention to give ecological consideration of niche or population in several species (Hynes, 1954; Croker, 1967; Sameoto, 1969a,b). Only a few, however, treated the life history in its morphological aspect. The present study deals with the results of investigation into the life history and breeding activity of *Orchestia platensis* in view to afford the basis for morphological discussion in the succeeding paper.

I am deeply indebted to Prof. E. Harada of the Seto Marine Biological Laboratory, for his encouragements and critical advices, and reading of the manuscripts. Dr. K. Sawada of Kyoto University kindly identified staphylinid beetles, to whom my thanks are due.

MATERIALS AND METHODS

Species Studied

Orchestia platensis is a nearly cosmopolitan sea-shore talitrid (Bousfield, 1973) that lives under the stranded matter in the supralittoral zone. Reported localities so far in the world are as follows; New Foundland to Florida in the Atlantic coast of North America (Bousfield, 1958, 1973), la Plata near Montevideo in South America (Stebbing, 1906), Bermuda Island (Kunkel, 1910), the West Indies (Bousfield, 1973) and the Canary Islands (Anderson, 1962) in the Atlantic Ocean; Denmark, Sweden,

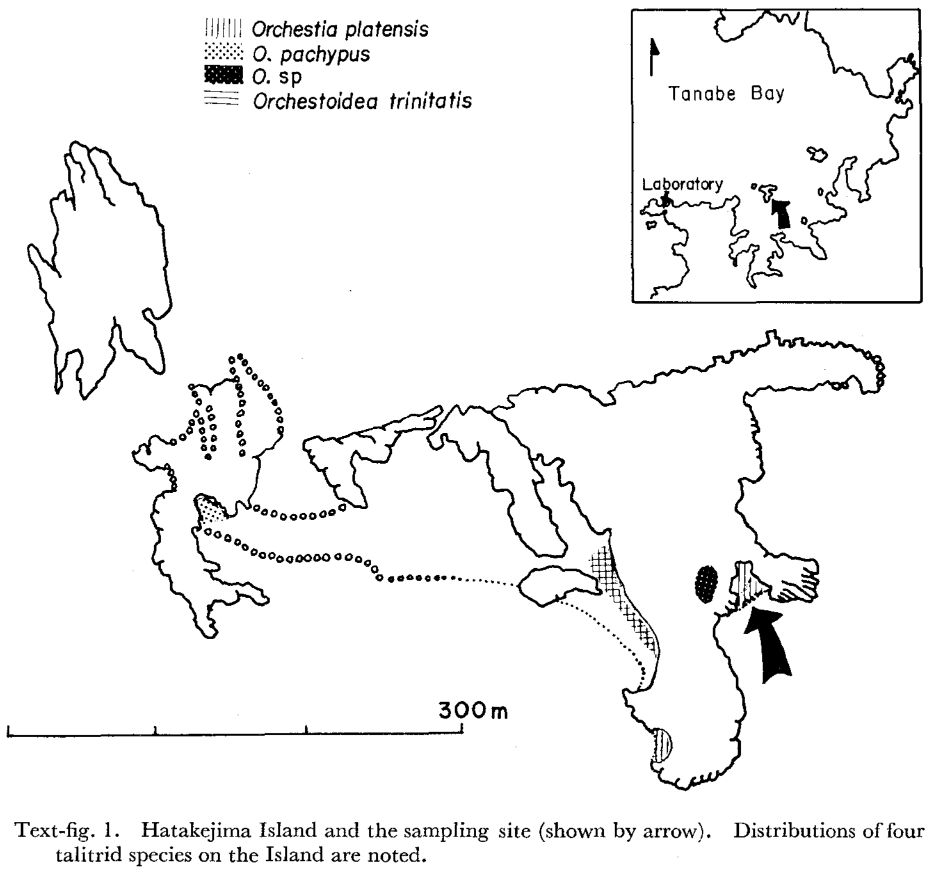
1) Contributions from the Seto Marine Biological Laboratory, No. 643.
2) Contributions No. 45 from the Itako Hydrobiological Station, Ibaraki University.

west Baltic and Mediterranean (Stephensen, 1944) in Europe: the Chilka Lake in India (Chilton, 1921), Sakhalin, Kuril Island (Bulycheva, 1957), Japan, Tansui in Formosa, Celebes Island (Ruffo, 1949) and Hawaii Island (Stephensen, 1935) in the North Pacific; and Bali, Tuamotsu Islands in the South Pacific (Stephensen, 1935). Of these localities, the Chilka Lake is brackish water and the habitat in Tenerife in the Canary Islands is a brook about 200 meters above the sea level.

In Japan, the species is commonly seen on the sandy shores from Hokkaido to Okinawa, and the microdistribution is strictly dependent on the occurrence of wrack bed (Morino, 1975). When the stranded matter was violently disturbed by the wave action in high tide or at typhoon, the animal was seen going up to land or burrowing in the sand. Results of field and experimental observations suggest that the species has omnivorous food habit.

Sampling Site and the Environment

A small sandy shore on the east coast of Hatakejima Island in Tanabe Bay (33°42′N, 135°22′W) was selected for the present study (Fig. 1). This shore is well isolated from the nearby sandy shores, being bordered by the rocky reefs on both sides

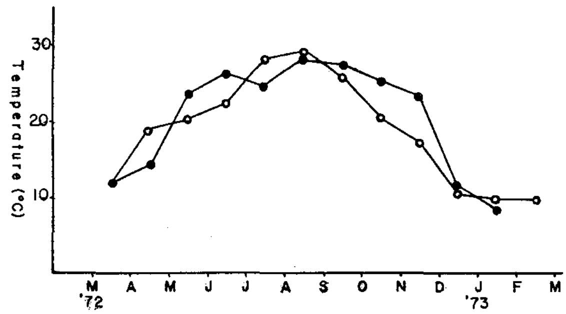


Text-fig. 1. Hatakejima Island and the sampling site (shown by arrow). Distributions of four talitrid species on the Island are noted.

and lined with bushes on landside. *Orchestia platensis* occurs in numbers on this shore, as well as on the sandy shore on the west side of the island, but active invasion or dispersion of *Orchestia platensis* into or from this shore seems to be negligible. Other three species of talitrids also occur on the island (Fig. 1). *Orchestoidea trinitatis* is seen on the sandy beach of the west side. *Orchestia pachypus* occurs on the limited sandy shore on a small isolated islet which is separated by a wide gravel flat from the main island. Under the litter in the forest right back of the sampling site, a terrestrial form of *Orchestia* sp. is found.

The organic matter found on the studied shore was chiefly stranded algae, woods, and dead fishes, as well as fallen leaves of pine trees on the island. The following animals were frequently caught with *Orchestia platensis* at the sampling site: Oligochaetes: *Pontdrilus matsushimensis*; Staphylinids beetles: *Emplenota fucicola, Phucobius simulator, Cafius nudus*; Crustacea: *Armadilloniscus tuberculatus, Alloniscus perconvexus, Ligia* (*Megaligia*) *exotica, Porcellio scaber, Exiroplana* (*Pontogeroides*) *japonica.* Parasitic mite was frequently found on the sternite or gills of *Orchestia platensis.*

The temperatures in the sand and under the stranded matter were measured with the aid of a thermister thermometer at each time of monthly samplings and the results are given in Fig. 2.



Text-fig. 2. Temperature fluctuations at the sampling site (solid circle), and in the laboratory (hollow circle).

Sampling Technique and Measurements.

Monthly samplings were carried out from March 1972 to March 1973. A sampler was devised by modifying a bottom sampler (15 cm × 15 cm). The sampler was pushed down onto the wrack bed to about 10 cm depth of the substratum sand and the content of the sampler was taken out with a shovel into a vinyl bag. Four sampling spots were selected according to the distribution of the stranded matter, so as to reflect the natural state of population as possible. In summer months, the stranded matter were frequently amassing on the hard substratum, that is, on the rocky reef or behind the sandy shore, where the stranded matter was also collected by use of hand from an area of about 15 cm × 15 cm.

The materials sampled were brought back to the laboratory and added with 10 % formalin for fixation of the animals. The animals were sorted out by decantation method of repeated procedure of adding, stirring and pouring out water until no animal was found in water. The remaining sand and wrack matter were also carefully examined. Extracted animals were preserved in 70 % alcohol.

The body length of *Orchestia platensis* was measured by micrometer from the tip of the head to the postero-median edge of pereionite VII by stretching the animal's back against a small board with the aid of a forceps and a needle under binocular microscope. The number of the flagellar segment of antenna II was counted on both sides. The sex was determined by the presence of oöstegite in female and the development of gnathopod II in male. The presence of the bristles on the oöstegite and egg number were checked. More than 20 thousands of animals were examined during the study.

Laboratory Observations

The laboratory observations were carried out in two lines. First, the life cycle and the seasonal change in breeding activity were followed under the room condition. Several pairs of mature animals were kept isolated in glass vessels (7 cm diameter and 18 cm height) with cotten wetted with sea water. The animals were inspected every day of the oviposition and the release of youngs. The number of the flagellar segments of antenna II were counted after every oviposition. The released youngs transferred to separate vessels were subsequently examined monthly of the number of the flagellar segments of antenna II and, if reached to maturation, of the reproductive activity as mentioned above.

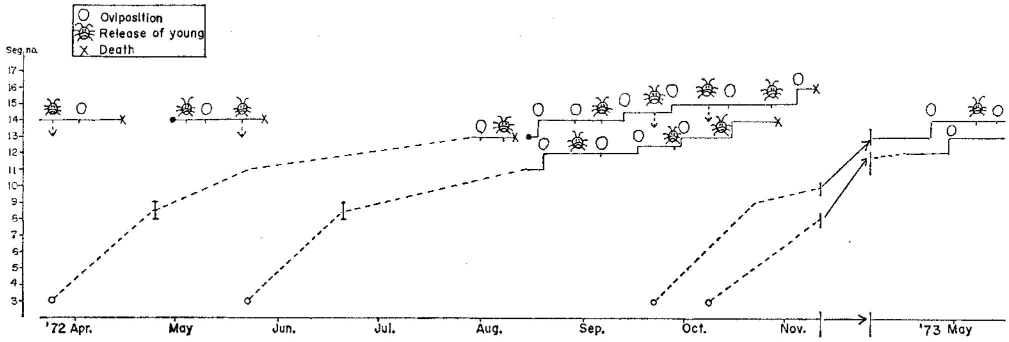
Secondly, the youngs hatched out in the laboratory were raised under the constant temperatures of 15°C, 20°C, 25°C and 30°C, and under the natural illumination. The animals were kept in the glass vessels separately, and the number of the flagellar segments of antenna II were examined individually every day. All the animals subjected to these observations were collected from the sampling site of Hatakejima Island.

RESULTS

1) Laboratory Studies

Life Cycle and Breeding Activity

Selected examples of growth, reproductive activity and life cycle in the room conditions are shown in Fig. 3. Youngs born in the spring commence breeding in the summer. The first oviposition can be predicted by the darkening of the gonad. Mature female, that is, female with dark gonad, is easily seized by male. Usually on the next day, eggs are deposited in the brood pouch During the development of the eggs in the brood pouch, the gonad becomes mature again. After releasing the youngs, the next batch is deposited. Some produce youngs in succession until late autumn when they die, and some cease breeding in autumn, overwinter and commence breeding again in the next spring. Overwintering female lacks bristles on



Text-fig. 3. Examples of growth and breeding activity through years in the laboratory. See text for detail.

the oöstegites. In some cases, particularly in mid summer, developing eggs in the brood pouch are lost before the youngs are produced. It is not certain whether this occurs naturally or accidentally and also in the nature or not.

Incubation and Successive Preoviposition Periods.

Incubation periods and successive preoviposition periods observed for the individuals of various numbers of flagellar segments of antenna II are summarized in Table 1. In spring and autumn, the incubation takes about 2 weeks and successive ovipositions occur about 20 days apart. In summer, the durations are shortened, one week and about 11 days for incubation and between successive oviposition respectively. Thus the durations fluctuate seasonally, though they does not show variation corresponding to segment number of antenna II, which is a molting age indicator, as mentioned below. So, the older does not neccessarily exhibit longer durations than the younger.

Growth and Increase in Segment Number of Antenna II

The newly hatched and released youngs bear three flagellar segments of antenna II on both sides. Daily inspection of the segment number revealed that the increase in number of flagellar segment occurred by adding the segment one by one on both sides simultaneously. It is very difficult to confirm the molting by the casted sheddings, which are usually eaten by the animal soon after sloughed off. However, it is most probable that each acquisition of one segment corresponds to a molt of the young because whenever exuviae were luckily remained in the vessel, the increase in segmental number occurred. This mode of addition of one segment at each molt seems to continue until maturation. Temperature specific durations in day of each segment number stage in young are given in Table 2.

The change in number of flagellar segments of antenna II counted immediately after each oviposition are shown in Table 3. Since this animal needs to molt prior to deposition of eggs, the numbers given in the table show the mode of increase of the flagellar segment at each molting after maturation during the breeding season.

Table 1. Seasonal variation of incubation period and successive preoviposition period under room condition.

Month	Antennal flagellar segment number	Incubaion period (days)	Successive preoviposition period (days)
Apr.	13		20
	14	17	
	14	14	23
	16	13	
	Average	15	22
May	13	15	
	14		15
	14	10	
	14	10	
	14	11	
	15	12	
	Average	12	15
Jun.	12	8	12
	13	10	
	15	12	
	Average	10	12
Jul.	13	7	10
	13	6	9
	13		11
	Average	7	11
Aug.	12	8	
	13	7	11
	13		12
	13		11
	13	7	
	14	8	15
	14	7	11
	14	8	12
	14	7	10
	14	8	14
	14		11
	15	7	12
	Average	7	12
Sept.	12		12
	13	11	13
	15	9	15
	15	11	16
	Average	10	14
Oct.	14	14	20
	14	18	
	15	13	20
	Average	15	20

Table 2. Periods in days needed for growth of the flagellar segment of antenna II of the young under different temperature regimes.

Temperature	Date of the release	Segment number of antenna II									
		3	4	5	6	7	8	9	10	11	12
30°C	Aug. 8 '72	3	2	4	4	5	5	9	4+		(jumped over)
	Aug. 8 '72	3	2	3	4	4	*	4	5+		
	Aug. 8 '72	3	3	3	6	4	4	6	7+		
25°C	Oct. 13 '73	5	5	6	6	5	5[1],5				
	Oct. 13 '73	5	4	5+							
	Oct. 23 '73	4	4	4	5	9	7+				
20°C	Oct. 13 '73	6	4	6	8	8	7	5+			
	Oct. 13 '73	5	2+								
	Oct. 13 '73	6	4	8	8	10	7+				
	Oct. 23 '73	5	4	6	9+						
15°C	Oct. 13 '72	10	10	11	11	16	30+				
	Oct. 13 '72	10	9	9	13	18+					
	Oct. 13 '72	11	10	15	25+						
	Oct. 13 '72	12	11	14	13+						

1) Left side segment number remained seven.

Table 3. Flagellar segment numbers of antenna II at successive ovipositions.

Date of the first oviposition	Numbers of flagellar segments at successive ovipositions. Left-right antenna II.							Date of the last oviposition
	Before	1st	2nd	3rd	4th	5th	6th	
Apr. 20 '73	13–13	14–14	14–14	14–14*	14–14	15–15		Jul. 16 '73
Apr. 26 '73	12–12	13–13	13–13	14–14				Jun. 5 '73
Jul. 30 '72	12–12	13–13	13–13	14–14	14–14	15–14	15–15	Oct. 15 '72
Aug. 23 '72	11–11	12–12	12–12	12–13	13–13	14–14		Oct. 13 '72
Aug. 27 '72	11–11	12–12	13–12	13–13				Oct. 3 '72
Aug. 3 '73	13–13	14–14	14–14	15–15				Aug. 26 '73
Sept. 20 '74	13–13	13–14	14–14	14–15				Oct. 19 '74
Sept. 25 '74	13–13	13–14	13–14					Oct. 9 '74

* In this case, oviposition did not occur, but the colour change showed molting.

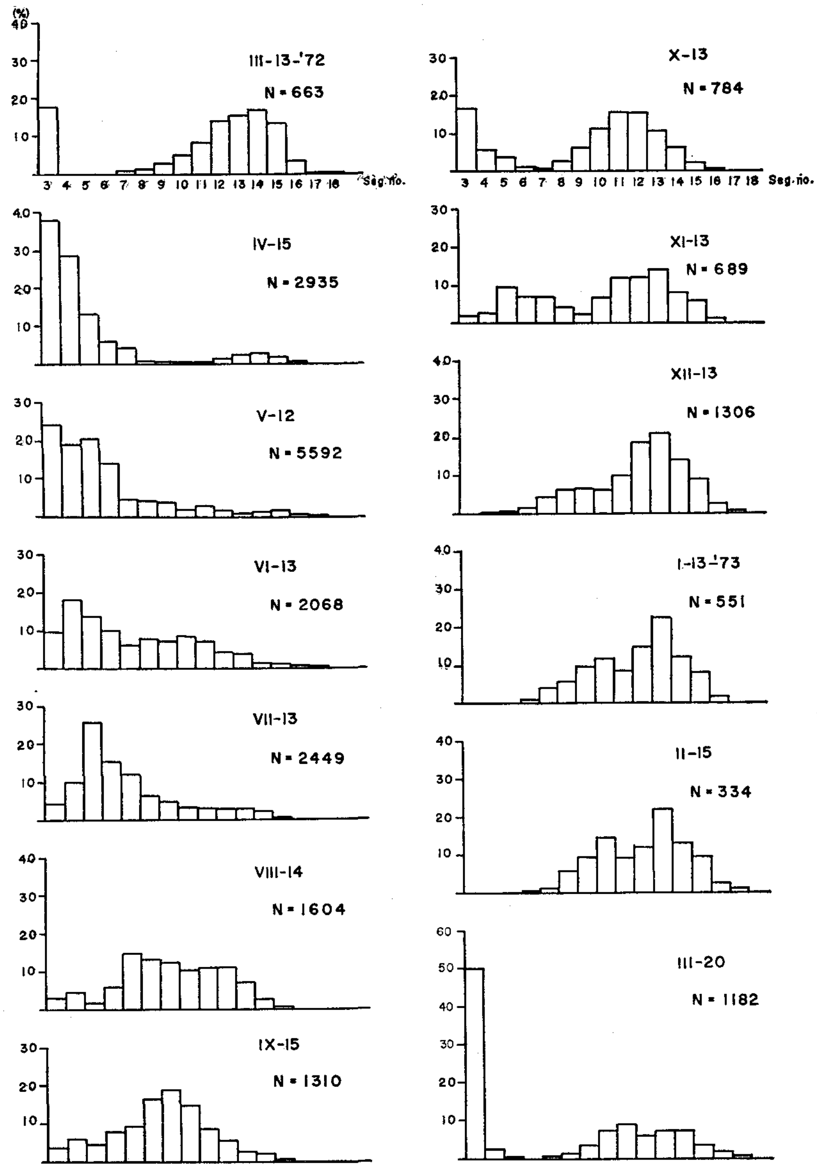
Usually they add one segment to the flagellum after two moltings simultaneously on both sides or alternatively on one side after the other. Accordingly, the same number of flagellar segments on both sides correspond to two successive molting ages and can not be attributed to either one of them, whereas any combinations of different number indicate decidedly the particular molting age.

2) Field Studies

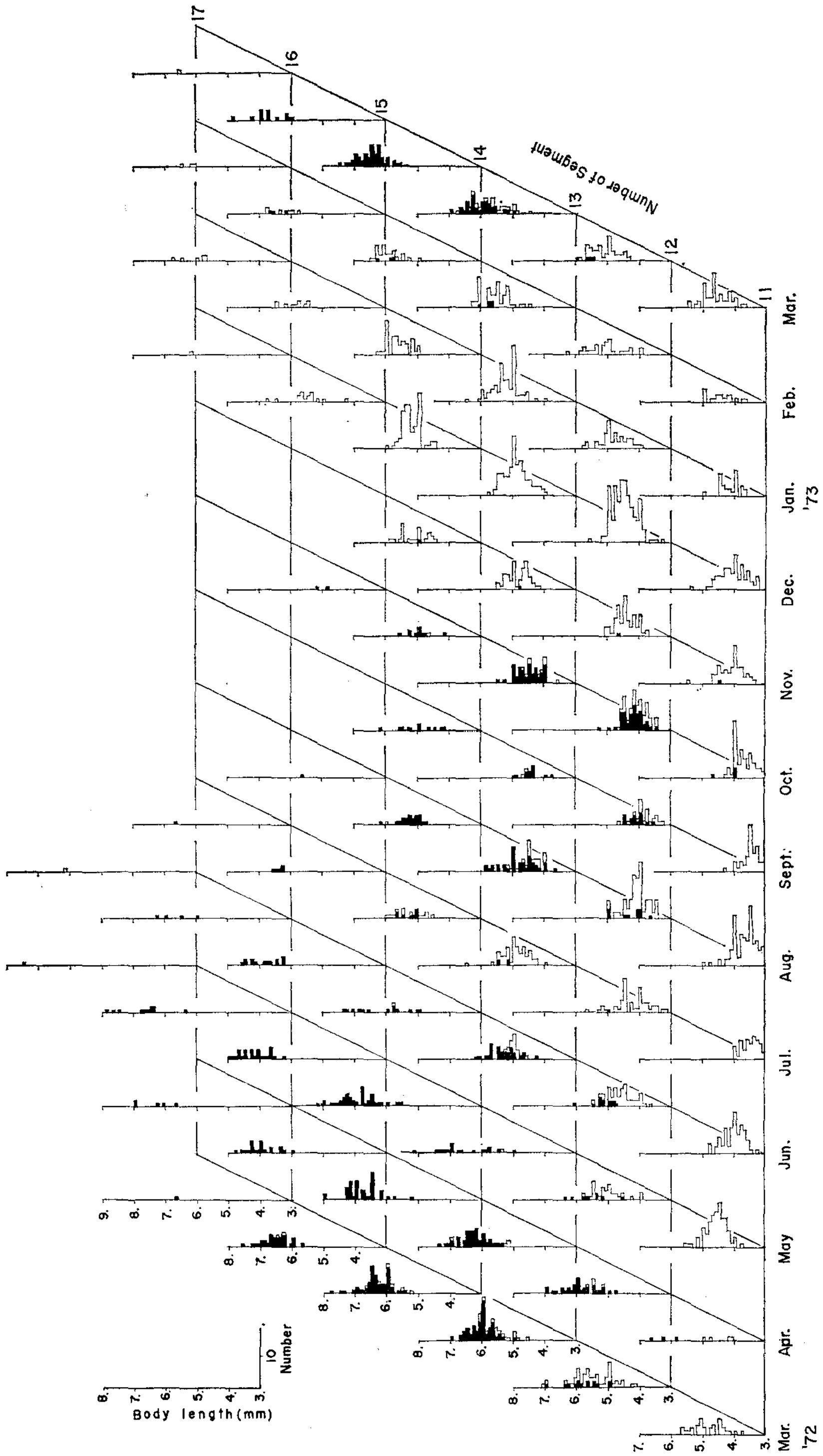
Life History

There was not a distinct difference in the population composition among four samples in each month, except in May when the stranded matter was distributed separately to form upper and lower belts. Two samples were taken from each belt in May and the samples from the upper belt contained much of larger animals and those from the lower belt were composed of mostly young animals.

Four samples of each month are put together and frequency distributions of flagellar segment number are shown in Fig. 4. The youngs with 3-segmented flagella of antenna II appear first in March. The youngs bearing antennal flagella less than



Text-fig. 4. Segment number frequency diagrams.



Text-fig. 5. Size frequency diagrams for the same segment number females. Breeding female (ovigerous or with fully developed bristles on oöstegite) are shadowed. See text for detail.

11 segments gradually increase in number and occupies the preponderant proportion of the population in April. From June to July, overwintered population disappears and a part of new year population replaces it, reaching to the ages with more than 11-segmented antennal flagella and starts to reproduce. The recruitment of the newly hatched youngs seems to fall down during the summer, but shows another peak, although not so pronounced as in the spring, in October, and continues until November. The late autumn population overwinters and starts breeding in the next spring.

Breeding Activity

Seasonal fluctuations in size frequency distribution of females and occurrence of breeding females are shown for each class of different segment number of antennal flagellum in Fig. 5. Female populations from December to June comprise much more individuals having more than 15 flagellar segments than those of the summer to autumn months. The modes of body size of the corresponding segment number classes are also evidently larger in the winter to spring populations than in the summer to autumn ones, gradually getting larger from August to April.

Breeding females, possessing fully developed bristles on the oöstegites, appear from February to November, mostly from March to October, but are very few in July populations. Apparent differences in the composition of flagellar segment number are recognizable for breeding females between March to May and August to October. Most of the breeding females in March to May, representing the overwintering population, bear more than 13-segmented antennal flagella and still many have more than 15-segmented ones, whereas the breeding females of the summer generation in August to October contain no or very few individuals having more than 15-segmented flagella and are composed almost entirely of those of 12 and 13 segment classes.

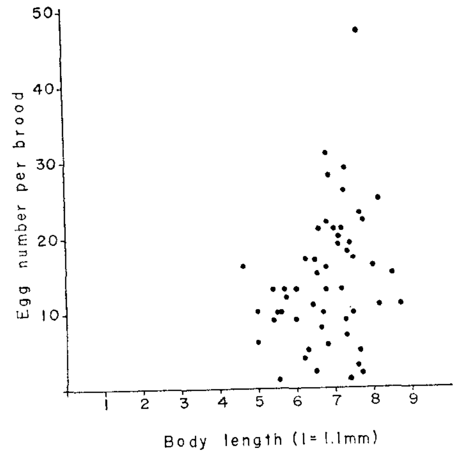
Egg Number per Brood and Egg Size

Egg number per brood varies from 1 to 47. Since disturbance during the sampling and the following procedures sometimes caused eggs to escape from brood pouch, the figures are apparently of underestimation. As shown in Fig. 6, larger females tend to produce more eggs per brood than smaller ones, which have been repeatedly said for other amphipodan species (Hynes, 1955; Kinne, 1950). The seasonal variation of the average egg number per brood is conspicuous (Table 4). Females of overwintering population produce much more eggs than those of the summer generation. Size difference of the female between these two populations, as mentioned above, might be one of the factors of the pronounced variation in egg number.

Egg size, measured along its long and short axis (Table 5), shows that overwintering population tend to produce larger eggs than autumn one.

Sex Ratio

Sex ratio, expressed as the number of females to a male and calculated for



Text-fig. 6. Relation between body length and egg number per brood in May.

Table 4. Monthly averages of egg number per brood

Month	Min.	Max.	Average±SD	Sample size
Mar.	1	23	12.52±4.18	119
Apr.	1	27	15.92±5.06	79
May	1	47	14.67±8.61	57
Jun.	2	17	9.35±4.08	20
Jul.	1	2	1.5	2
Aug.	1	5	3 ±2	5
Sept.	1	6	4.14±2.12	7
Oct.	2	9	5.47±2.11	32

Table 5. Egg diameters of spring and autumn broods

Month	Egg diameter (mm) ±SD		Sample size
	long axis	short axis	
Mar.	0.68±0.04	0.52±0.02	40
Apr.	0.70±0.04	0.54±0.02	32
Sept.	0.59±0.02	0.45±0.03	7
Oct.	0.66±0.05	0.51±0.02	38

individuals larger than 4.4 mm in body length, varies between 1.1 and 2.7 (Table 6). Female dominates male in all months, but there is no distinct tendency in the variation of sex ratio.

Table 6. Sex ratio. Treated animals are larger than 4.4 mm in body length.

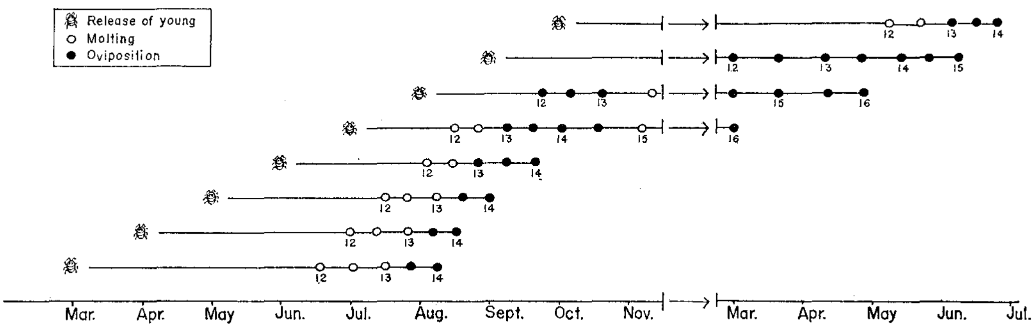
Month	Female	Male	Female : Male
'72 Mar.	272	191	1.4 : 1
Apr.	164	137	1.2 : 1
May	289	176	1.6 : 1
Jun.	203	74	2.7 : 1
Jul.	114	76	1.5 : 1
Aug.	144	87	1.7 : 1
Sept.	42	38	1.1 : 1
Oct.	122	93	1.3 : 1
Nov.	148	118	1.3 : 1
Dec.	475	364	1.3 : 1
Jan.	255	129	2.0 : 1
Feb.	146	72	2.0 : 1
'73 Mar.	265	149	1.8 : 1

Average 1.6 : 1

DISCUSSION

General Consideration on Life History of Orchestia platensis

Life history and breeding activity of the Shirahama populations are diagrammatically presented in Fig. 7. This figure is constructed as follows; growth in terms of segment number increase is deduced by the prevailing seasonal temperature and temperature specific growth of the segment, as well as the seasonal variation of successive preoviposition periods. Reproductive activity and life span are estimated from segment frequency diagram. For example, female population released in April are reckoned to grow to have 12-segmented antennal flagella in early July. In September they would be 15-segmented. But Fig. 4 shows no 15-segmented female in this month, so they are thought to die before then. Fig. 5 shows high percentage of immature 12-segmented females in July, and most of 13-segmented females being in breeding in August. Thus the population released in April produces two successive



Text-fig. 7. Hypothetical diagram showing growth, reproductive activity and yearly cycles of field population. See text for detail.

broods of eggs in their lives. Youngs born in March grow slowly and in early summer attain to 12-segmented, and breeding begins when they attain to 13 or 14-segmented stage to produce a few broods. Those born in May grow less slowly and commence breeding in mid summer, but produce a few broods, too. These populations which become adult in summer are small in body length and mortalities are rather high. That is to say, the adults are recruited rapidly, but they produce only a small number of eggs and die soon. Youngs in July and August grow rapidly and begin to breed so soon as in October and enter into reproductive resting period. In next spring they produce a few brood again. Those born in late summer and October compose the main overwintering population. In winter, there seems to be no increase in flagellar segment number, although growth in the body length occurs to some degree, as is shown in Fig. 5. Comparison of the modes of size frequency diagrams between November and January in 12 or 13-segmented females shows about 10 % growth during these months. This figure seems to correspond to growth in one molt or less. In decapodan larvae, growth between instars range from about 0 % to 170 %, and have a mode between 10 % and 20 % (Rice, 1968). Some adult females seem to molt one time and some do not during the resting period, which is not recognizable in the segment frequency diagram. These overwintered large females can produce much more eggs of large size, as well as much more broods than summer generation.

In regard to population maintenance, winter must be a critical period, because breeding ceases, and only mortality exists. The condition adverse to population is compensated by the continual growth of overwintering population during winter, which results in production of a large number of eggs in the next spring to regain the population. Thus the resting period seems to have a character of vegetative phase for the population.

Seasonal Variation of Life History and Environmental Conditions

As has been stated above, life history phenomena, such as growth, breeding activity and life span, of *O. platensis* show seasonal variation. In this section, the varying life history is examined in relation to seasonal changes of environmental conditions.

Life history diagram is presented in Fig. 7. The youngs from the animals having passed through the resting period appear in March when the temperature is still rather low. They grow continually during spring-summer period when the temperature is rising and start breeding in mid summer when they reach 13 or 14 flagellar segment stage. So, it takes about 4 months for them to resume breeding state. Gradual acceleration of growth and maturation is seen in the youngs appearing later than March. Youngs born in August spend hottest season in their early lives and start breeding in autumn at 12 flagellar segment stage. In this case, it takes only about 2 months for the first oviposition. Some of them enter into the resting period in November when the temperature is still high. Those generations produced in mid summer and early autumn spend their adult stage in winter. Darkening in colour of the gonad suggested that many of them were getting matured in Junuary, the coldest season of the year. Youngs born in autumn live their early lives in winter and grow to mature in the following spring. All these overwintering populations exhibit thus longer life span than the summer generation.

The variation in life span is thus attributable to the difference in growth speed and the presence or absence of resting period. The resting period of winter may be attained and spent after or before reaching the breeding stage, consequently extending the breeding period, respectively. The resting period and slower growth are apparently related to lower temperature, and the acceleration of growth to higher temperatures. Breeding is, however, not so much related to temperature, so far as the seasons when breeding occurs are concerned, if various generations are all taken into consideration, nor to some particular short periods of the year, not suggesting the day and night length effects. The commencement of breeding is also not necessarily bound to the attainment to a certain definite number of molts nor to some determined body size, as is shown in Fig. 5.

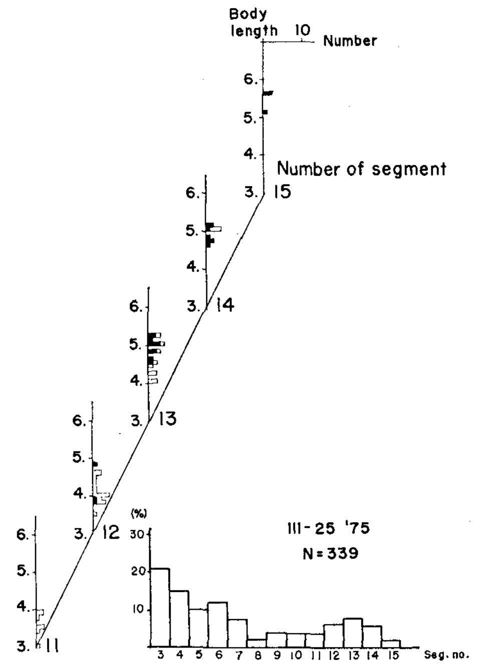
So, in the course of repeated production of generations, fluctuating temperature may retard or accelerate the growth and initiate or cease the resting period, that seems to be the principal nature of the existence of the seasonal variation of life history in this species. For growth, food factor is assumed to be important, but in the present case, there were always good quantity of organic stranded matter on the shore and this factor may be regarded to have little effect on this seasonal variation in life history.

Geographical Variation of Life History of Orchestia platensis

Bock (1967) investigated the life history of this species in Flensburger Förde in Germany (54°50'N, 9°50'W). The general life history pattern of the Flensburger population is similar to Shirahama population, in spite of great latitudinal difference between these two localities. According to Bock, overwintered population begins to breed in March and a large part of them continues to breed until July when they die. The new generation matures in May and terminates breeding in November. The breeding season, therefore, extends from March through November with two peaks of reproductive activities in April and June. Longer breeding season and sooner maturation of new generation of Flensburger population than in Shirahama are seemingly incompatible with latitudinal difference between two localities. Geographical variation of temperature specific parameters of life history events which correlate inversely with latitude may explain this discrepancy. Indeed, Bock's rearing experiment shows that a constant temperature of 20°C raised the animal to maturation in 8 weeks. On the other hand, Shirahama population matures in about 11 weeks under the same temperature, and it is under 30°C that the animal matures in about 8 weeks.

According to Dahl (1946), the breeding season of *O. platensis* in Holland begins in May and ends in November. During the season, three peaks of the reproductive activity are recognized. He thought that the first peak in June was attained by the overwintered population and the following two peaks were due to new generations. Thus the general pattern is like those of Shirahama and Flensburger population, except the existence of the third peak of reproductive activity in Holland. Dahl explained it by the warm autumn climate in the locality.

This leads naturally to the question what is occurring in the population of the southern region. In order to get some information on this point, a sampling was carried out in Azama, Okinawa Pref. (26° 10′N, 127°50′W) in March, by the same method as adopted in Shirahama, where the mean atmospheric temperature was about 19°C in this month. The flagellar segment number frequency distribution and the proportion of breeding female are shown in Fig. 8. The population structure is similar to that of May, not of March, in Shirahama. At least, breeding commences long before March, but existence of two modes clearly shows that the reproductive activity decreased in the foregoing season. It is not certain whether the resting



Text-fig. 8. A sample in Azama, Okinawa Ken.

period exists or not. At the same time, comparison of size composition of the same segment stage between Okinawa and Shirahama population (Fig.5) shows that the size of Okinawa population in March is much smaller than that in Shirahama population of the same month. Size variation in the same segment stage is also noticeable seasonally in Shirahama population (see Fig. 5), namely, smaller in summer than in winter. Both geographical and seasonal variations of the size suggest the effect of temperature on the size. Higher temperature accelerates molting and shortens intermolt period. Shorter intermolt period might decrease the growth per molt. In addition, resting period may play some role in the variation of growth per molt, since overwintered population in Shirahama is largest in the year. Thus difference

Table 7. Gammarid species and the life history types.

Family	Species	Habitat	Locality	Type	Remarks	Source
Gammaridae	*Gammarus duebeni*	estuary	Holyrood, Conception Bay, Nfld	3		Steele and Steele (1969)
		mouth of stream	Gansey beach, Isle of Man, England	3		Hynes (1954)
		small stream	Port Erin Stream, Isle of Man	1	Youngs decrease in Oct.-Jan. and Jul.-Aug.	Hynes (1954)
		brackish lake	Kleinen kiel, Kiel, Germany	3		Kinne (1952)
		lake	Storvatnet lake, Trondelag, Norway	3		Solen (1969)
	G. fasciatus	drainage dykes	Frodsham marsh, Cheshire, England	2		Hynes (1955)
	G. finmarchicus	intertidal zone	St. Andrews, New Brunswick, Canada	1	Small females elaspe resting period.	Steele and Steele (1975b)
	G. lacustris lacustris	lake	Llyn Llywenan, Anglesey, England	3		Hynes (1955)
	G. l. limnaeus	stream	St. Lawrence River, U.S.A.	4		Hynes and Harper (1972)
	G. lawrentianus	estuary	Holyrood, Conception Bay, Nfld	2		Steele and Steele (1970c)
	G. obtusatus	intertidal zone	St. Philips, Conception Bay, Nfld	3		Steele and Steele (1970b)
	G. oceanicus	intertidal zone	Holyrood, Conception Bay, Nfld	3		Steele and Steele (1972a)
	G. pseudolimnaeus	river	Credit Forks, Ontario, Canada	3		Hynes and Harper (1972)
	G. pulex pulex	stream	Shotwick, Cheshire, England	2		Hynes (1955)
	G. setosus	intertidal zone	New Foundland area, Canada	3		Steele and Steele (1970a)
	G. tigrinus	estuary	Pottery Brock, St. Andraus, Nfld	3		Steele and Steele (1972b)
	G. wilkitzki	under permanent ice	Arctic region	3		Steele and Steele (1975a)
	Crangonyx gracilis	river	Llangollen, Denbighsire, England	1		Hynes (1955)
	C. richmondensis lawrentianus	lake	Algonquin Park, Canada	3		Sprules (1967)
		pond	Redmond Pond, Ontario, Canada	3		Judd (1963)
	Marinogammarus marinus	intertidal zone	Kattendijke, Oosterschelde, Holland	3		Vlasblom (1969)
	Calliopius laevisculus	intertidal zone	St. Philips, Conception Bay, Nfld	2		Steele and Steele (1973b)
		intertidal zone	Labrador	3		Steele and Steele (1973b)
	Anisogammarus annandalei	lake	Lake Biwa, Shiga Prefecture, Japan	3	Inshore population breeds in spring. Offshore in autumn.	Narita (1975)
	Gammarellus angulosus	intertidal zone	Dyers Gulch, Logy Bay, Nfld	3		Steele and Steele (1972c)
	Melita zeylanica	brackish lake	Veli Lake, Terata, India	1		Krishnan and John (1974)

Hyalellidae	*Hyalella azteca*	lake	Surgarlraf Lake, Michigan, U.S.A.	2		Cooper (1965)
		hot spring	Central Oregon, U.S.A.	1		Strong (1972)
	Austrochiltonia subtenuis	brackish lake	West Victoria, South Australia	1	Youngs increase in March and October.	Lim and Williams (1971)
	Parhyalella pietschmanni	intertidal zone	Nosy Bé, Madagascar	1		Steele and Steele (1973)
Talitridae	*Orchestia platensis*	supralittoral zone	Shirahama, Wakayama Prefecture, Japan	2		Present paper
		supralittoral zone	Flensburger Förde, Germany	2		Bock (1960)
	O. sp	terrestrial	Mito, Ibaraki Prefecture, Japan	3	Spring and autumn subpopulations exist.	Tamura and Koseki (1974)
	O. bottae	terrestrial	Leiden, Holland	2		Dorsman (1935)
	Talitrus tasmaniae	terrestrial	Tasmania, New Zealand	1	Youngs decrease in winter.	Friend (personal communication)
Ampeliscidae	*Ampelisca abdita*	subtidal sandy bottom	Barnstable Harbour, Canada	2		Mills (1963)
	A. vadorum	subtidal sandy bottom	Long Island Sound, Canada	2		Mills (1963)
	A. brevicornis	subtidal sandy bottom	Helgoland Bight, Germany	3		Klein *et al.* (1975)
	A. macrocephala	subtidal sandy bottom	Helsinger, Knahaken, Norway	4		Kanneworff (1965)
Corophiidae	*Corophium volutator*	esturaine mad flat	River Dovey, North Wales, England	2		Watkins (1941)
Haustoriidae	*Bathyporeia pilosa*	subtidal sandy bottom	Ynyslas Cardiganshire, England	1	Youngs increase in May and October.	Fish and Preece (1970)
	B. pelagica	subtidal sandy bottom	Ynyslas Cardiagnshire, England	2		Fish and Preece (1970)
	Haustorius canadensis	subtidal sandy bottom	Cape Cad, Canada	3		Sameoto (1969a)
	Neohaustorius biarticulatus	subtidal sandy bottom	Cape Cad, Canada	3		Sameoto (1969a)
	N. schmitzi	subtidal sandy bottom	Radio Island, North Carolina, U.S.A.	2		Dexter (1971)
	Parhaustorius longimerus	subtidal sandy bottom	Cape Cad, Canada	3		Sameoto (1969b)
	Pontoporeia affinis	coastal water (3 m depth)	Trarmine, Finland	3		Segerstråle (1950)
		coastal water (35 m depth)	Trarmine, Finland	4	Four year old population exists.	Segerstråle (1950)
		lake	Sognsvann, Norway	4		Mathisen (1953)
		shallow lake	Mälaren, Stockholm, Sweden	3		Wiederholm (1973)
		central lake	Mälaren, Stockholm, Sweden	4		Wiederholm (1973)

of local climate seems to explain the geographical variations of life history between Okinawa and Shirahama populations.

Patterns of Life History Phenomena in Gammaridean Amphipoda

Fairy many amphipodan species have been treated in terms of breeding biology and life history by many investigators. In this section, available informations are reviewed to get the general idea on the life history phenomena of gammaridean amphipods, and to compare them with the results of the present study.

Modes of the breeding activity and life history are classified into the following four types.

Breeding throughout the year	Type 1
Breeding restricted seasonally	
Two generations completing a yearly life cycle	Type 2
One generation completing a yearly life cycle	Type 3
Two years or more necessary for breeding	Type 4

This classification is a tentative one and there are naturally some species of intermediate types, which are noted in remarks of Table 7 showing the species with their habitats and localities for each type.

The type is somewhat correlated with the latitude of the localities of the species belonging to it, but not with their systematic categories nor habitats. Tropical species, such as *Melita zeylanica* in Veli lake, India and *Parhyalella pietschmann* in Madagascar, show life histories of type 1. Hot spring population of *Hyalella azteca* is also of type 1. Continuous high ambient temperature permits the species to breed throughout the year. Some species, such as *Bathyporeia pilosa, Gammarus duebeni* in Port Erin Stream and *G. finmarchicus* breed throughout the year in high latitudes. However, the reproductive activities of them decrease in winter, or the individual variation of growth is extraordinary in the life history of *Crangonyx gracilis* (Hynes, 1955). On the contrary, type 4 species are restricted to much higher latitudes in distribution. Most of the species of temperate region belong to type 2 or 3. Accordingly, in global scale, it can be admitted that low latitude species tend to breed throughout the year and have short life span, and high latitude species are apt to have long life span and breed in a restricted season.

Intraspecific or subspecific variations of the life history type are frequently met with, as seen in *Gammarus duebeni, Hyalella azteca, Pontoporeia affinis* and *Gammarus lacustris*. Hynes (1954) assumed temperature difference to correspond to the variation of life history in *G. duebeni* between Port Erin Stream and Gansey Beach. Variation of life history of *Hyalella azteca* is also ascribed to temperature. Strong (1973) reported for *H. azteca* that hot spring population followed the life history of type 1, as noted above, though stream population near the hot spring restricted its breeding season. Fish and Preece (1970) stressed the localized factors involved as well in the geographical populations of *Bathyporeia pilosa* on the west coast of France, namely, a northerly located population reproduced throughout the year, and a southern population shows a single reproductive cycle. Ökland (1969) examined the breeding seasons of *Gammarus lacustris* in various localities in Norway and mentioned that the northern populations did not always retard the start of the breeding activity. Therefore temperature can not be regarded as a sole factor which governs the variation of reproductive activity among geographical populations. Local factors, such as food aboundance (Wiederholm, 1973), and the geographical variation of the physiological properties among populations, as seen in *Orchestia platensis,* may be associated with.

Orchestia platensis belongs to type 2, which is common in this region investigated. According to Tamura and Koseki (1974), a related terrestrial species *Orchestia* sp.* pass through the life history of type 3, and has two subpopulations, that is, spring subpopulation which breed from May through July and autumn subpopulation which breed from late July through September. It is most probable that the terrestrial *Orchestia* was derived from supralittoral *Orchestia* directly (Hurley, 1959; Morino, 1972) and the semi-cosmopolitan species, for example *O. platensis,* could be the stock species (Hurley, 1959). If it can be assumed that associated changes in some factors with migration from supralittoral to terrestrial evnironment causes slow growth, as has been suggested by Wildish (1972), the life history of type 2 of *O. platensis* could be quite easily converted into that of type 3 of *O.* sp. Overwintering population and new year generation of the former species may be taken as corresponding to autumn subpopulation and spring one of the latter, respectively Modification of life history, as is established as geographical variation in life history in many species as shown above, may not be difficult problem as well in the case of invading different new habitat .

Summary

1. Life history and breeding activity of *Orchestia platensis* Krφyer were studied by rearing and by monthly collecting of field populations from March 1972 to March 1973 on Hatakejima Island, Shirahama, Wakayama Prefecture.
2. In the laboratory, youngs born in spring started breeding in summer. Those born in late summer or autumn stopped breeding to overwinter until next spring.
3. Duration of incubation and successive preoviposition period fluctuated seasonally, about 2 weeks in spring population, 7 to 11 days in mid-summer population and about 20 days in autumn population.
4. Young animals added their flagellar segments of antenna II one by one at each molting. In adult, two molts were needed to add one flagellar segment.
5. In the field collections, breeding females were found mainly from March to October. The breeding activity of the population showed two peaks, in spring and in autumn. Youngs appeared in March began to breed in early summer with 12-segmented antennal flagella. The overwintered population disappeared thereafter. Youngs born in early summer matured in autumn, spent resting period in

* Tamura and Koseki (1974) referred to the species as *O. platensis japonica*

winter, and commenced breeding again in the following spring, bearing mostly more than 13 antennal flagellar segments. Thus, at least two generations were required to complete a yearly life cycle.

6. Larger females tended to produce more eggs per brood, up to 47, and larger ones than those produced by smaller females. Female dominates male in all seasons.

7. Life history and breeding activity of Shirahama population were compared with those in Okinawa, Germany and Holland, and the geographical variation among them were discussed.

8. Life histories reported for gammaridean amphipods were reviewed and categorized into 4 types, with some considerations on ecological features of the species belonging to them. The possibility of modification from one type to another were discussed in relation to habitat change during land invasion in the talitrid species.

REFERENCES

Andersson, Å. 1962. On a collection of Amphipoda of the family Talitridae from the Canary Islands. Arkiv för Zoologi, Bd. 15, Nr. 11, pp. 211–218.

Andronikov, V.B. 1975. Heat resistance of gametes of marine invertebrates in relation to temperature conditions under which the species exist. Mar. Biol., Vol. 30, No. 1, pp. 1–11.

Amanieu, M. 1969. Cycle reproducteur à Archachon d'une population de *Orchestia gammarella* (Pallas) (Amphipode Talitridae). Bull. Inst. océanogr. Monaco, Vol. 68, No. 1390, pp. 1–24.

Bock, K-D. 1967. Experimente zur Ökologie von *Orchestia platensis* Krøyer Z. Morph. Ökol. Tiere, Vol. 58, pp. 405–428.

Bousfield, E.L. 1958. Distributional ecology of the terrestrial Talitridae (Crustacea: Amphipoda) of Canada. 10th International Congress Entomol. Proc. for 1956, Vol. 1, pp. 883–898.

Bulycheva, A.I. 1957. Morski blohi morej SSSR is sopredelnysk vod (Amphipoda-Talitroidea). Opred. po Faune SSSR, Akad, Nauk SSSR, Vol. 65, 185 pp. 66 text-figs. (In Russian)

Charniaux-Cotton, H. 1975. Contrôle hormonal de la differenciation sexuelle et de l'activité génitale chez les crustacés malacostracés. Pubbl. Staz. zool. Napoli, Vol. 39, Suppl. 1, pp. 480–509.

Chilton, C. 1921. Fauna of the Chilka Lake, Amphipoda. Mem. Indian Mus., Vol. 5, pp. 519–558.

Cooper, W.E. 1965. Dynamics and production of a natural population of a fresh-water Amphipoda, *Hyalella azteca*, Ecol. Monogr., Vol. 35, No. 4, pp. 377–394.

Croker, R.A. 1967. Niche diversity in five sympatric species of intertidal Amphipods (Crustacea: Haustoriidae). Ecol. Monogr., Vol. 37, No. 3, pp. 173–200.

Dahl, E. 1946. The Amphipoda of the Sound. Part 1. Terrestrial Amphipoda. Lunds Univ. Arsskrift, N.F. Aud. 2, Bd, 42, Nr. 6. pp. 1–52.

De March, B.G.E. 1977. The effects of photoperiod and temperature on the induction and termination of reproductive resting stage in the freshwater amphipod *Hyalella azteca* (Saussure). Can. J. Zool., Vol. 55, No. 10, pp. 1595–1600.

Dexter, D.M. 1971. Life history of the sandy-beach amphipod *Neohaustorius schmitzi* (Crustacea: Haustoriidae). Mar. Biol., Vol. 8, pp. 232–237.

Dorsman, B.A. 1935. Notes on the life-shitory of *Orchestia bottae* Milne Edwards. Diss. inaug. Leyden, 58 pp.

Duncan, K.W. 1969. The ecology of two species of terrestrial Amphipoda (Crustacea; Family Talitridae) living in waste grassland. Pedobiologia, Bd. 9, pp. 323–341.

Fish, J.D. and G.S. Preece. 1970. The annual reproductive patterns of *Bathyporeia pilosa* and *B. pelagica*. J. mar. biol. Ass. U.K., Vol. 50, pp. 425–488.

——— 1975. Development, hatching and brood size in *Bathyporeia pilosa* and *B. pelagica* (Crustacea Amphipoda). J. mar. biol. Ass. U.K., Vol. 55, pp. 357–368.

Giese, A.C. 1959. Comparative physiology: Annual reproductive cycles of marine invertebrates.

Ann. Rev. Physiol., Vol. 21, pp. 547–576.
——— and J.S. Pearse. 1974. Reproduction of Marine Invertebrate. Vol. 1, Acoelomate and Pseudocoelomate Metazoans. 546 pp. Academic Press, New York and London.
Gledhill, T. and M. Ladle. 1969. Observations on the life-history of the subterranean amphipod *Niphargus aquilex* Schoite. Crustaceana, Vol. 16, pp. 51–56.
Hurley, D.E. 1959. Notes on the ecology and environmental adaptations of the terrestrial Amphipoda. Pac. Sci., Vol. 13, No. 2, pp. 107–129.
——— 1968. Transition from water to land in amphipod Crustaceans. Am. Zoologist, Vol. 8, pp. 327–353.
Hynes, H.B.N. 1954. The ecology of *Gammarus duebeni* Lilljeborg and its occurrence in fresh water in western Britain. J. Anim. Ecol., Vol. 23, pp. 38–84.
——— 1955. The reproductive cycle of some British freshwater Gammaridae. J. Anim. Ecol. Vol. 24, pp. 352–387.
——— and F. Harper. 1972. The life histories of *Gammarus lacustris* and *G. pseudolimnaeus* in southern Ontario. Crustaceana, Suppl. 3, pp. 329–341.
Irie, H. 1967. Breeding and life cycle of Amphipoda. Inform. Bull. Planktol. Japan, No. 14, pp. 25–32.
Judd, W.W. 1963. Studies of the Byron Bog in south-western Ontario XVI. Observations on the life cycle of two species of *Crangonyx* (Crustacea: Amphipoda). Nat. Hist. Papers, Natl. Museum Can., No. 20, pp. 1–9.
Kanneworff, E. 1965. Life cycle, food and growth of the amphipod *Ampelisca macrocephala* Lilljeborg from Öresund. Ophelia, Vol. 2, No. 2, pp. 319–322.
Kinne, O. 1952a. Zum Lebenszyklus von *Gammarus duebeni* Lillj.; Nebst einigen Bemerkungen zur Biologie von *Gammarus zaddachi* Sexton subsp. *zaddachi* Spooner. Veroff. Inst. Meeresforsch. Bremerhaven, Bd. 1, pp. 187–203.
——— 1952b. Zur Biologie und Physiologie von *Gammarus duebeni* Lillj., V: Untersuchungen über Blutkonzentration, Herzfrequenz und Atmung. Kieler Meeresforsch., Bd. 9, Hf. 2, pp. 134–150.
——— 1953a. Zur Biologie und Physiologie von *Gammarus duebeni* Lillj., IV: Über den Ruhezustand (Reduktion der Oöstegiten-borsten). Zool. Anz., Bd. 150, Hf. 3/4, pp. 41–49.
——— 1953b. Zur Biologie und Physiologie von *Gammarus duebeni* Lillj., VI: Produktionsbiologische Studie. Veroff. Inst. Meeresforsch. Bremerhaven, Bd. 2, pp. 135–145.
Klein, G., E. Rachor and S.A. Gerlach. 1975. Dynamics and productivity of two populations of the benthic tube dwelling amphipod *Ampelisca brevicornis* (Costa) in Helgoland Bight. Ophelia, Vol. 14, pp. 139–160.
Krishnan, L. and P. A. John. 1974. Observations on the breeding biology of *Melita zeylanica* Stebbing, a brackish water amphipod. Hydrobiologica, Vol. 44, No. 4, pp. 413–430.
——— and ——— 1975. Breeding biology of the amphipod *Melita zeylanica* Stebbing in a tropidal monsoonal lake. Zool. Anz., Bd. 194, Hf. 5/6, pp. 328–334.
Ladle, M. 1975. The Haustoriidae (Amphipoda) of Budle Bay, Northumberland. Crustaceana, Vol. 28, Pt. 1, pp. 37–47.
Lim. K.H. and W.D. Williams. 1971. Ecology of *Austrochiltonia subtenuis* (Sayce) (Amphipoda, Hyalellidae). Crustaceana, Vol. 20, Pt. 1, pp. 19–24.
Mathisen, O.A. 1953. Some investigations of the relict crustaceans in Norway with special reference to *Pontoporeia affinis* and *Palasea quadrispinosa*. Nytt Mag. Zool., Vol. 1, pp. 49–86.
Menor, P.S. 1969. Population ecology of *Gammarus lacustris* Sars in Big Island Lake. 1. Habitat preference and relative abundance. Hydrobiologia, Vol. 33, pp. 14–32.
Mills, E.L. 1967. The biology of an ampeliscid amphipod crustacean sibling species pair. J. Fish. Res. Bd. Canada, Vol. 24, No. 2, pp. 305–355.
Morino, H. 1972. Studies on the Talitridae (Amphipoda, Crustacea) in Japan I. Taxonomy of *Talorchestia* and *Orchestoidea*. Publ. Seto Mar. Biol. Lab., Vol. 21, No. 1, pp. 43–65.
——— 1975. Ditto II. Taxonomy of sea-shore *Orchestia*, with notes on the habitats of Japanese sea-shore talitrids. *Ibid.*, Vol. 22, Nos. 1/4, pp. 171–193.
Narita, T. 1976. Occurrence of two ecological forms of *Anisogammarus annandalei* (Tattersal) (Crus-

tacea: Amphipoda) in Lake Biwa. Physiol. Ecol. Japan, Vol. 17, Nos. 1/2, pp. 541–546.

Ökland, K.A. 1969. On the distribution and ecology of *Gammarus lacustris* G.O. Sars in Norway, with notes on its morphology and biology. Nytt Mag. Zool., Vol. 17, pp. 111–152.

Rüppel, G. 1967. Zur Lokomotionsaktivität des Amphipoden *Orchestia platensis* in Freiland und im Laboratorium. Helgolander wissenschaftliche Meeresuntersuchungen, Bd. 15, Hf. 1/4, pp. 172–180.

Sameoto, D.D. 1969a. Comparative ecology, life histories, and behavior of intertidal sand-burrowing amphipods (Crustacea: Haustoriidae) at Cape Cod. J. Fish. Res. Bd. Canada, Vol. 26, No. 2, pp. 361–388.

——— 1969b. Some aspects of the ecology and life cycle of three species of subtidal sand-burrowing amphipods (Crustacea: Haustoriidae). *Ibid.*, Vol. 26, No. 5, pp. 1321–1345.

Scientific Annual. 1975. Tokyo Astronomical Station (ed.) Maruzen Ltd.

Segerstråle, S.G. 1950. The amphipods on the coasts of Finland. Some facts and problems. Soc. Scient. Fenn. Comm. Biol., Vol. 10, No. 14, pp. 1–28.

——— 1970. Light control of the reproductive cycle of *Pontoporeia affinis* Lindström (Crustacea Amphipoda). J. exp. mar. Biol. Ecol., Vol. 5, pp. 272–275.

——— 1971. Light and gonad development in *Pontoporeia affinis*. Fourth European Marine Biology Symposium. Ed. by D.J. Crisp. Cambridge.

Sexton, E.W. and A. Mattews. 1913. Notes on the life history of *Gammarus chevreuxi*. J. mar. biol. Ass. U.K., Vol. 9, pp. 546–556.

Solen, J.O. 1969. Ecology of *Gammarus duebeni* Lilljeborg in a Norwegian lake. D.K.N.V.S. Skrifter, Nr. 2, pp. 3–12.

Steele, D.H. and V.J. Steele. 1969. The biology of *Gammarus* (Crustacea, Amphipoda) in the northwestern Altantic I. *Gammarus duebeni* Lillj. Can. J. Zool., Vol. 47, No. 2, pp. 235–244.

Steele, V.J. and D.H. Steele. 1970a. Ditto II. *Gammarus setosus* Dementieva. *Ibid.*, Vol. 48, No. 4, pp. 659–671.

Steele, D.H. and V.J. Steele. 1970b. Ditto III. *Gammarus obtusatus* Dahl. *Ibid.*, Vol. 48, No. 5, pp. 989–995.

——— and ——— 1970c. Ditto IV. *Gammarus lawrentianus* Bousfield. *Ibid.*, Vol. 48, No. 6, pp. 1261–1267.

Steele, V.J. and D.H. Steele. 1972a. Ditto V. *Gammarus oceanicus* Segerstråle *Ibid.*, Vol. 50, No. 6. pp. 801–813.

Steele, D.H. and V.J. Steele. 1972b. Ditto VI. *Gammarus tigrinus* Sexton. *Ibid.*, Vol. 50, No. 8, pp. 1063–1068.

——— and ——— 1972c. Biology of *Gammarellus angulosus* (Crustacea, Amphipoda) in the northwestern Atlantic. J. Fish. Res. Bd. Canada, Vol. 29, No. 9, pp. 1337–1340.

——— 1972d. Some aspects of the biology of *Gammarellus homari* (Crustacea, Amphipoda) in the northwestern Atlantic. *Ibid.*, Vol. 29, No. 9, pp. 1340–1343.

——— and V.J. Steele. 1973a. The biology of *Gammarus* (Crustacea, Amphipoda) in the northwestern Atlantic. VII. The duration of embryonic development in five species at various temperatures. Can. J. Zool., Vol. 51, No. 9, pp. 995–999.

——— and ——— 1973b. Some aspects of the biology of *Calliopius laevisculus* (Krøyer) (Crustacea, Amphipoda) in the northwestern Atlantic. *Ibid.*, Vol. 51, No. 7, pp. 723–728.

——— 1973c. The biology of *Parhyalella pietchmanni* Schellenberg, 1938 (Amphipoda, Hyalellidae) at Nosy Bé, Madagascar. Crustaceana, Vol. 25, Pt. 3, pp. 276–280.

——— and V.J. Steele. 1975a. The biology of *Gammarus* (Crustacea Amphipoda), in the northwestern Atlantic IX. *Gammarus wilkitzkii* Birula, *G. stoerensis* Reid and *G. mucrontus* Say. Can. J. Zool., Vol. 53, No. 8, pp. 1105–1109.

——— and ——— 1975b. Ditto X. *Gammarus finmarchicus* Dahl. *Ibid.*, Vol. 53, No. 8, pp. 1110–1115.

——— and ——— 1975c. Ditto XI. Comparison and discussion. *Ibid.*, Vol. 53, No. 8, pp. 1116–1126.

Strong, D.R. 1972. Life history variation among populations of an amphipod (*Hyaella azteca*). Ecology, Vol. 53, No. 6, pp. 1103–1111.

Sprules, W.G. 1967. The life cycle of *Crangonyx richmondensis lawrentianus* (Crustacea: Amphipoda). Can. J. Zool., Vol. 45, pp. 877–884.

Tamura, H. and K. Koseki. 1974. Population study on a terrestrial amphipod, *Orchestia platensis japonica* (Tattersal), in a temperate forest. Jap. J. Ecol., Vol. 24, No. 2, pp. 123–139.

Vlasblom, A.G. 1969. A study of a population of *Marinogammarus marinus* (Leach) in the Oosterchelde. Neth. J. Sea Res., Vol. 4, No. 3, pp. 317–338.

Watkin, E.E. 1941. The yearly life cycle of the amphipod *Corophium volutator*. J. Anim. Ecol., Vol. 10, pp. 77–93.

Wiederholm, T. 1973. On the life cycle of *Pontoporeia affinis* (Crustacea Amphipoda) in Lake Mälaren. Zoon, Vol. 1, pp. 147–151.

Wildish, D.J. 1972. Post embryonic growth and age in some littoral *Orchestia* (Amphipoda, Talitridae). Crustaceana, Suppl. 3, pp. 267–274.